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Megalopal and first crab stages of *Porcellanopagurus edwardsi* Filhol, 1885 (Crustacea: Decapoda: Anomura: Paguridea)

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Abstract.—The megalopal and first crab stages of a hermit crab believed to be *Porcellanopagurus edwardsi* Filhol, 1885, are described and illustrated from specimens collected off New Zealand during the U.S. Antarctic Program, 1962–1968. This is the first report of post-larval development in the genus. While the megalopal stage of *P. edwardsi* is generally quite similar to megalopae of other described pagurid genera, a significant difference is seen in the first crab stage. At this stage in most pagurids there typically is reduction in the second pleopods on both sides of the abdomen; the remaining right side pleopods may be reduced or lost entirely, whereas left side pleopods usually undergo only endopod reduction or loss. In contrast, all pleopods of *P. edwardsi* undergo dramatic reduction with the molt to the first crab stage.

Of the 11 species now recognized in the hermit crab genus *Porcellanopagurus* Filhol, 1885a, for none have larvae ever been reared in the laboratory. However, four zoeal stages of *Porcellanopagurus edwardsi* Filhol, 1885b, were described by Roberts (1972) from plankton samples collected in Perseverance Bay, Campbell Island, New Zealand, the type locality of the species. The present post-larval series, containing four megalopae and three first stage crabs was collected during the U.S. Antarctic Program's USNS *Eltanin* cruise 25 at station 370 (43°22′–43°24′S, 175°20′–175°15′E, 95 m, 19 Nov 1966). This area coincides with the reported southern extent of the range of *Porcellanopagurus filholi* de Saint Laurent & McLaughlin, 2000 and the northern limits of the range of *P. edwardsi* (cf. de Saint Laurent & McLaughlin 2000).

Although these two species of *Porcellanopagurus* were confounded under the name *P. edwardsi* for more than a century, adults are readily distinguishable by several characters, particularly the lateral carapace lobes, rostral shapes, and length-width proportions of the ambulatory dactyls and pereopods. Lateral carapace lobes are not present in the megalopal stage and have not reached their full developmental potential during the first crab stage. Similarly, length-width proportions of the ambulatory dactyls and pereopods are expected to be subject to change with growth. No larval or post-larval information is available for *Porcellanopagurus filholi*; however, the similitude seen between the developing rostrum in the megalopa and in first crab stage of the present material and the characteristic subadult-adult rostrum of *P. edwardsi* (Fig. 1a) provide reasonable assurance of the identity of these early stages.

The post-larval specimens used in this study have been deposited in the alcohol and slide reference collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 276169), as have the majority of the small but morphologically mature specimens used for anatomical comparisons. Two megalopae and one first crab stage were stained with chorazol black E, dis-

sected, and mounted in polyvinyl alcohol lactophenol. Whole specimens were examined, drawn, and dissected using a Wild M-5 microscope with camera lucida attachment. Slides were examined and appendages drawn using a Wild M-20 microscope with camera lucida attachment. Information was also obtained from the examination of adult specimens of both *Porcellanopagurus* species belonging to the New Zealand Oceanographic Institute, now part of the National Institute of Water and Atmospheric Research, Wellington, New Zealand. The interpretation of lateral carapace lobes, particularly the tripartite condition of the posterior carapace lobe as defined by of McLaughlin (2000) is applied to the descriptions of the crab stage. Thoracic sternites are indicated by Roman numerals according to the system used by Pilgrim (1973). In other terminology, the recommendations of Clark et al. (1998), as applicable to anomurans, have been adopted. Two measurements, carapace length (cl) and shield length (sl) are used as indicators of specimen size.

Description

Megalopa

Size.–cl = 2.0–2.5 mm; n = 4.

Carapace (Fig. 1b).—Shield only faintly indicated; lateral carapace margins smoothly contoured. Rostrum obtusely subtriangular, apex produced, terminating acutely or subacutely. Anterolateral angles of shield (incipient lateral projections) slightly produced and upturned. Ocular peduncles moderately short, corneas slightly dilated; ocular acicles not apparent.

Thoracic sternites (Fig. 1e).—Sternite of third maxillipeds (sternite IX) with anterior margin rounded on either side of median cleft, not distinctly fused with sternite of chelipeds (X). Sternites X and XI partially fused. Sternite XII with incomplete median longitudinal depression or groove. Sternite XIII moderately broad, separated from preceding sternite by thin flexible uncalcified hinge. Sternite XIV separated from XIII by membranous area.

Antennule (Fig. 3a).—Biramous, considerably overreaching ocular peduncles; peduncle 3-segmented, basal segment with statocyst faintly apparent and with 5 or 6 short lateral setae, 1 long and 2 shorter stiff setae ventrally and sometimes 1 short seta dorsally; penultimate segment usually without setae; ultimate segment with 1 or 2 short setae dorsally and ventrally; endopod (lower ramus) 2-segmented; basal segment with 3 or 4 short setae distally, distal segment with 4–6 short and 2 appreciably longer setae; exopod (upper ramus) 4-segmented, distal segment longer than combined length of first 3, aesthetascs on segments 2–4 as follows: 6, 4–6, 4, penultimate segment often also with 1 or 2 long setae distally, ultimate segment with 3–5 short and 1 long terminal setae.

Antenna (Fig. 2a).—Peduncular segments 3–5 each with 0–2 short setae; second segment with dorsolateral distal angle produced as short spinose process, dorsomesial distal angle rounded; first segment with unarmed ventral protuberance. Acicle short, broad, with 2–4 short setae. Flagella, long, with 20–22 articles each often with 1 or 2 short setae, terminal article with 3 or 4 short and 1 or 2 considerably longer setae.

Mandible (Fig. 2c).—Reduced and simplified, distal margin unarmed or with small tooth; palp 2-segmented, distal segment with 5–9 very short marginal setae.

Maxillule (Fig. 2e).—Coxal endite with 5 or 6 plumose marginal setae; basial endite with 3 or 4 marginal weakly plumose setae dorsally, row of several small teeth on outer margin and adjacent row of few widely-spaced short setae; endopod unsegmented, with short seta subdistally.

Maxilla (Fig. 2g).—Coxal endite bilobed, with 5–7 marginal plumose setae on proximal lobe and 4–6 on distal lobe; basial endite bilobed, with 6–8 plumose marginal setae on proximal lobe and 10–12 plumose marginal setae on distal lobe; endopod unsegmented, with 1 subterminal and 1 termi-

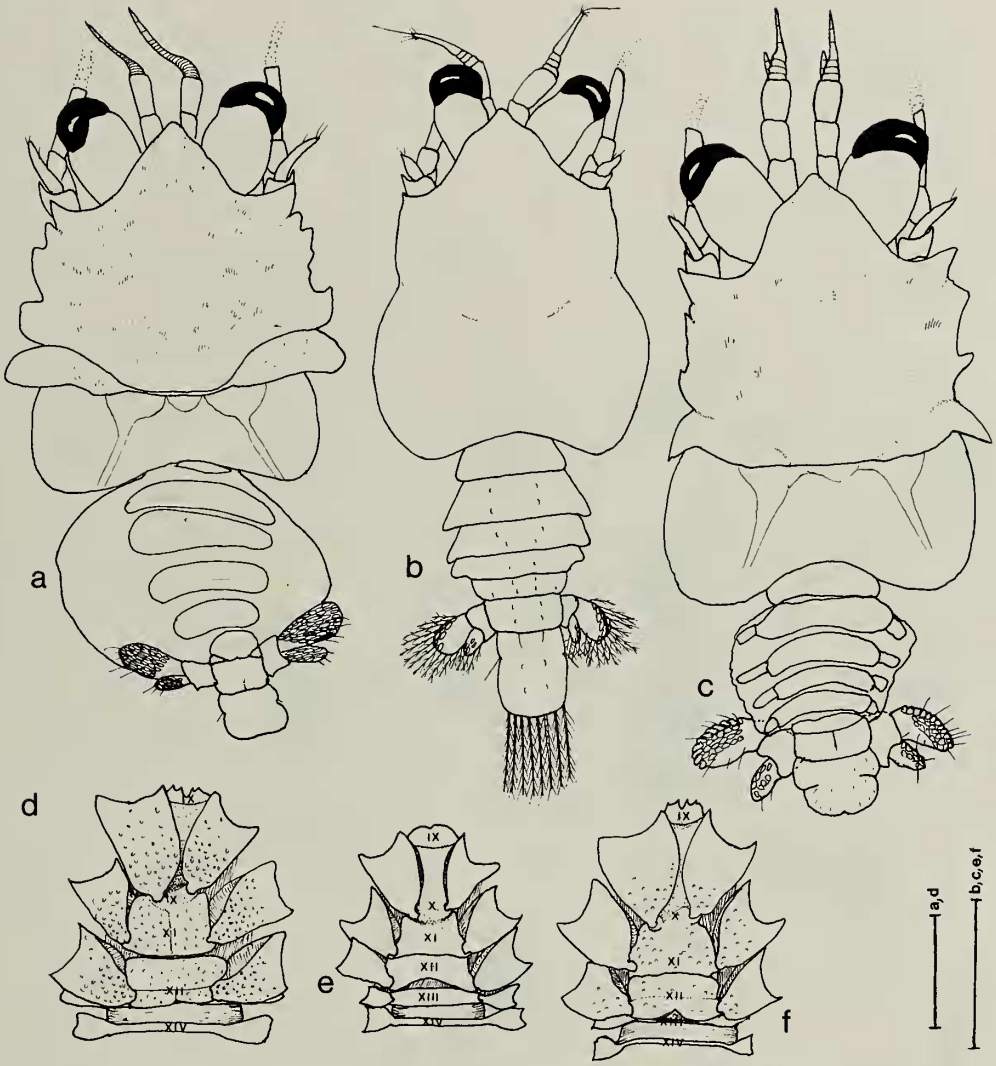

Fig. 1. *Porcellanopagurus edwardsi* Filhol, 1885. a–c, cephalothorax and abdomen (dorsal view); d–f, thoracic sternites (ventral view): a, d, young adult male (sl = 2.3, cl = 3.0 mm, Eltanin cruise 27, stn 1850, 49°40′S, 178°53′E, 103 m, 3 Jan 1967); b, e, megalopa (cl = 2.2 mm); c, f, first crab stage (sl = 1.9, cl = 2.3 mm). Scales equal 1.0 mm.

nal simple seta; scaphognathite with 44–52 moderately short, marginal plumose setae.

Maxilliped 1 (Fig. 2i).—Coxal endite with 2 or 3 simple or weakly plumose setae marginally and sometimes 1 additional seta submarginally; basial endite with 13–15 short marginal plumose setae; endopod unsegmented, 0–2 very short setae terminally and 1 or 2 simple setae on inner margin; exopod indistinctly 2-segmented, distal segment with 0–1 very short seta.

Maxilliped 2 (Fig. 3c).—Endopod 4-segmented, basal segment with 1 short seta, penultimate segment with 1 or 2 short simple setae, ultimate segment with 4 or 5 terminal simple or plumose setae; exopod 2-segmented, distal segment with 6 long plumose setae.

Fig. 2. *Porcellanopagurus edwardsi* Filhol, 1885. a, c, e, g, megalopa (cl = 2.2 mm); b, d, f, h, first crab stage (sl = 1.9, cl = 2.3 mm): a, b, antennal peduncle; c, d, mandible; e, f, maxillule; g, h, maxilla; i, j, first maxilliped. Scale equal 0.25 mm.

Maxilliped 3 (Fig. 3e).—Endopod 5-segmented, all segments with numerous setae, those of ultimate and penultimate segments most frequently serrated or barbed; accessory tooth of developing crista dentata apparent; exopod 2-segmented, distal segment with 6 long terminal plumose setae.

Pereopods (Fig. 4a, c, e, g, i).—Chelipeds unequal, right larger. Cutting edge of dactyl of right with 2 strong calcareous

Fig. 3. *Porcellanopagurus edwardsi* Filhol, 1885. a, c, e, megalopa (cl = 2.2 mm); b, d, f, first crab stage (sl = 1.9, cl = 2.3 mm): a, b, antennule; c, d, second maxilliped; e, f, third maxilliped. Scale equal 0.25 mm.

teeth, terminating in corneous claw; chela with faint ridge on dorsolateral margin; carpus and merus each with few low protuberances or short ridges dorsally; ischium unarmed. Cutting edges of dactyl and fixed finger of left with corneous teeth, terminating in corneous claws; chela unarmed; carpus and merus each with few low protuberances on dorsal surfaces; ischium unarmed. Both chelae with few scattered setae. Ambulatory legs generally similar, dactyls of second and third pereopods each with row of 8 corneous spinules on ventral margins, propodi each with 2 widely-spaced spiniform setae on ventral margins and 2 at or near ventrodistal margin; carpi and meri each with row of few low protuberances setae on dorsal surface. Fourth pereopods semi-chelate with propodal rasp of 1 row of corneous scales; dactyl long, curved; all segments with 1-several scattered setae. Fifth pereopods chelate; with few corneous scales on outer surface and margin of propodus, distal margin with 2 or 3 long curved setae; carpus and merus also with 1 or 2 short simple setae.

Abdomen (Fig. 1b).—Tergites of 6 somites all chitinous, unarmed but with 2 or 3 pairs of short setae as illustrated. Unequally biramous pleopods (Fig. 4k–n) on

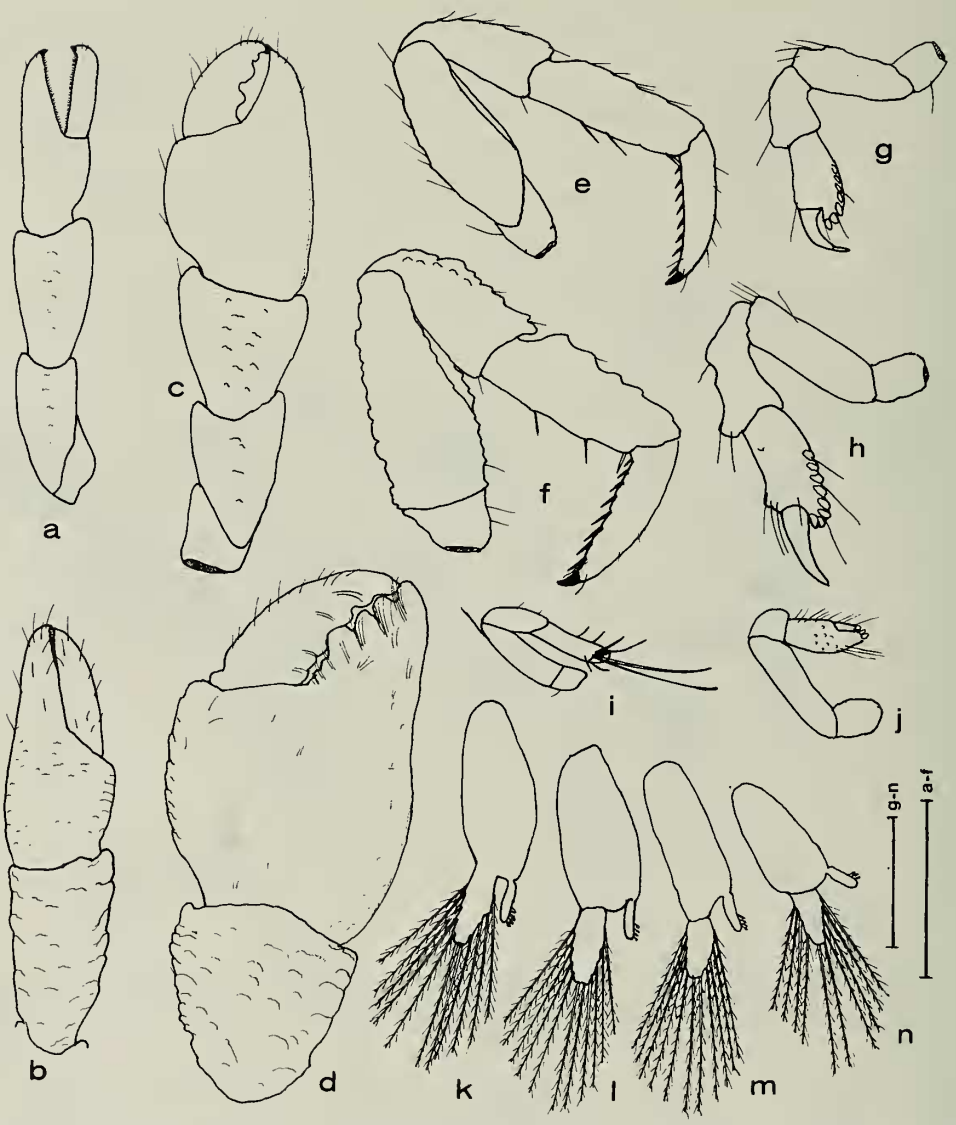

Fig. 4. *Porcellanopagurus edwardsi* Filhol, 1885. a, c, e, g, i, k–n, megalopa (cl = 2.2 mm); b, d, f, h, j, first crab stage (sl = 1.9, cl = 2.3 mm): a, left cheliped (dorsal view); b, carpus and chela of left cheliped (dorsal view); c, right cheliped (dorsal view); d, carpus and chela of right cheliped (dorsal view); e, f, right second pereopod (lateral view); g, h, left fourth pereopod (lateral view); i, j, right fifth pereopod (lateral view); k–n, left pleopods 2–5 respectively. Scales equal 0.5 mm (g–n) and 1.0 mm (a–f).

somites 2–5, exopods of second through fourth each with 11, fifth 10 marginal plumose setae; endopods each with appendix interna consisting of 4 (endopods 2–4) or 3 (fifth) apical hooks. Uropods (Fig. 1b) symmetrical; protopods with 1–3 setae on dorsal surface; exopods 1-segmented, with 15 or 16 simple and plumose setae marginally, 13–15 corneous scales on outer and terminal margins collectively, endopods short, each with 6 or 7 setae and 4–6 corneous scales. Telson with small lateral indentations each accompanied by 1 moderately long seta anterior to mid-length; 2 pairs of

short setae on dorsal surface; terminal margin rounded and with 4 + 4 long plumose setae.

Gills.—Arthrobranchs well developed on chelipeds and pereopods 2–4, rudimentary on third maxillipeds.

First Crab

Size.—sl = 1.8–1.9 mm; cl = 2.2–2.4 mm; n = 3.

Carapace (Fig. 1c).—Shield with cervical groove partially to completely delineated, approximately as long as broad (lateral lobes of shield included); dorsal surface with few scattered setae. Posterior carapace with lateral lobes partially to completely delineated, produced beyond level of anterior carapace lobes, directed posteriorly and terminating acutely; no median element developed; posterolateral and posteromedian plates weakly calcified, *cardiac sulci* and *sulci cardiobranchialis* delinated. Rostrum very well developed, occupying at least half anterior margin, obtusely triangular and terminating subacutely; spiniform lateral projections developing anterolaterally. Ocular peduncles short, stout; corneas not dilated; ocular acicles developing as calcified thickenings at peduncular bases, obscured from dorsal view by rostrum.

Thoracic sternites (Fig. 1f).—Sternites IX–XII all with numerous small surface tubercles or granules. Sternites IX (third maxillipeds), X (chelipeds) and XI (second pereopods) now all fused, but suture lines still apparent. Sternite XII (third pereopods) now with transverse median furrow. Sternite XIII (fourth pereopods) now transposed to position posteroventral to XII. Separation of XIV from preceding sternites slightly greater.

Antennule (Fig. 3b).—Peduncle little changed from previous stage; exopod 6-segmented, aesthetascs on second–fourth segments as follows: 6, 6, 4, fourth segment also with 2 short setae distally, ultimate segment with 4 or 5 terminal setae; endopod 3-segmented; basal segment with 2 or 3 moderately long setae; penultimate segment with 1 very long distal seta; terminal segment with 5 or 6 short setae.

Antenna (Fig. 2b).—Fifth and fourth peduncular segments with few setae; third segment with 1 strong spine on ventral margin, second segment little changed from previous stage, first segment unarmed; acicle still subrectangular, with minute terminal spinule and 2 or 3 setae. Flagella missing.

Mandible (Fig. 2d).—Larger and often more strongly calcified but otherwise unchanged; distal segment of palp with 14–17 very short marginal setae.

Maxillule (Fig. 2f).—Coxal endite with several plumodenticulate and 12–16 plumose and simple, submarginal and/or marginal setae; basial endite with 2 rows of teeth and few simple or plumose setae marginally and 4 simple setae submarginally, 3 or 4 additional plumose or simple setae on inner margin; protopod with 3 prominent setae on outer margin; endopod with internal lobe slightly produced and with 1 moderately long bristle, external lobe obsolete.

Maxilla (Fig. 2h).—Coxal endite bilobed, with 10–15 marginal plumose and plumodenticulate setae and row of submarginal plumose setae extending onto lower margin on proximal lobe, distal lobe with 6 or 7 marginal and 5 or 6 submarginal plumose setae; basial endite bilobed, with 7–10 plumose marginal setae on proximal lobe and 9 or 10 marginal and 1 or 2 submarginal plumose setae on distal lobe; endopod with 2 subterminal simple setae; scaphognathite with approximately 75 moderately short, marginal plumose setae.

Maxilliped 1 (Fig. 2j).—Coxal endite with 7 or 8 plumose or plumodenticulate setae marginally; basial endite with 20–30 marginal plumose and plumodenticulate setae and submarginal row of simple or weakly plumose setae; endopod with 8 or 9 plumose setae on inner margin; exopod 2-segmented, distal segment with 1 subterminal simple and 6 terminal plumose setae, prox-

imal segment with 5–8 plumose setae on outer margin.

Maxilliped 2 (Fig. 3d).—Endopod 5-segmented, with setation as illustrated; exopod 2-segmented, distal segment still with 6 or 7 long plumose and 2 short simple setae, proximal segment with 1 seta adjacent to outer margin and 1 proximally near inner margin.

Maxilliped 3 (Fig. 3f).—Endopod 5-segmented, all segments with increased number of setae, more on ultimate and penultimate segments often serrate or barbed; merus with prominent spine at dorsodistal margin, crista dentata with 10–12 teeth and strong accessory tooth; exopod 2-segmented, proximal segment with 1 stiff bristle on outer margin and 2 on or adjacent to inner margin and 1 on outer face, distal segment still with 8 long terminal plumose and 3 shorter, subterminal simple setae.

Pereopods (Fig. 4b, d, f, h, j).—Right cheliped much stronger than left; cutting edges of dactyl and fixed finger of right each with few strong calcareous teeth; palm with row of low faint ridges on dorsomesial margin, few low ridges on dorsolateral margin and scattered setae on dorsal surface; carpus low, scale-like protuberances on dorsal surface, somewhat stronger similar protuberances on dorsomesial margin and dorsolateral margin; merus with scattered granules on dorsal surface, dorsomesial margin with several short transverse ridges, ventromesial margin with row of strong spines; ischium with row of spines on ventromesial margin. Left cheliped with cutting edges of dactyl and fixed finger with several corneous teeth, terminating in corneous claws; palm with scattered low ridges and minute granules, dorsomesial and dorsolateral margins each with few low ridges; carpus with scale-like protuberances or ridges on dorsomesial and dorsolateral margins, dorsal surface with several short transverse ridges; merus with short transverse ridges dorsally, row of subacute spines on ventromesial margin; ischium with row of prominent subacute spines on ventromesial margin. Ambulatory legs larger, dorsal margins of meri, carpi and propodi now with much more prominent protuberances on dorsal surfaces, carpi each with row of protuberances on lateral face in dorsal half. Fourth pereopods larger but not appreciably changed from previous stage. Fifth pereopods with few more granular-like scales on propodal surface.

Gills.—Increased in size and complexity; no pleurobranch apparent.

Abdomen (Fig. 1c).—Noticeably shortened and swollen; tergites of somites 1–6 somewhat reduced from previous stage; paired, but markedly reduced uniramous pleopods still present on somites 2–5, all lacking setation.

Telson and uropods (Fig. 1c).—Telson with scattered short setae on dorsal surface; transverse suture partially developed; terminal margin with weak median indentation. Uropods symmetrical; protopods each usually with small projection posteriorly; exopods with numerous plumose setae, dorsal surfaces each with 4 or 5 rows of corneous, spiniform scales; endopods each with double row of corneous scales and few short setae.

Discussion

The megalopal stage of *Porcellanopagurus edwardsi* is generally quite similar to megalopae of other described pagurid and diogenid species, except for the marked prominence of the rostrum and lack of a well defined shield. In these characters, *P. edwardsi* might mistakenly be perceived as a lithodid (e.g., *Hapalogaster*, cf. Konishi 1986: fig. 3M; *Placetron*, cf. Crain & McLaughlin 2000b, fig. 1C). Of course with the molt to first crab, the distinctiveness of *Porcellanopagurus* becomes apparent. The lateral carapace lobes begin to develop, the shield becomes delineated, and the lateral projections begin to take on their characteristic prominence. Thoracic sternites IX–XII develop the typically broad, flattened aspect of the adult (Fig. 1d), and

the joint facets of the chelipeds become distinctly asymmetrical. Sternite XIII moves to a posteroventral position beneath XII, while sternite XIV remains a very slender rod-like structure widely separating the coxae of the fifth pereopods. The development of six segments in the antennular exopod is comparable to that reported by McLaughlin et al. (1989) for some specimens of *Pagurus kennerlyi* (Stimpson, 1864), although a five-segmented exopod is more common in pagurid crab stage 1 (Carvacho 1988, Ingle 1990, McLaughlin et al. 1992, Crain & McLaughlin 1994, Gherardi & McLaughlin 1995).

More profound differences are seen in the abdomen of the first crab stage of *P. edwardsi*. In the typical pagurid abdomen, the megalopal tergites are considerably reduced, if not lost almost entirely, with segmentation becoming indistinct, or marked simply by transverse fibrils, although some exceptions have been noted in *Discorsopagurus* (cf. Gherardi & McLaughlin 1995). In *P. edwardsi*, some reduction in the size of the individual tergites can be observed, but segmentation is clearly indicated. Additionally, while the typical pagurid abdomen remains elongate and slightly to strongly twisted, or at least flexed, the abdomen of *P. edwardsi* becomes noticeably shortened, with accompanying lateral expansion to give a semi-globular shape. The most significant difference between *P. edwardsi* and the described first crab stages of species of *Pagurus*, *Anapagurus*, *Discorsopagurus*, even the parapagurid genus *Sympagurus*, and the diogenid genera of *Clibanarius*, *Paguristes*, and *Dardanus* (cf. Lemaitre & McLaughlin 1992, McLaughlin et al. 1993, for specific reviews) is seen in the pleopods. Although second pleopods on both sides of the abdomen are typically reduced in most of the above cited genera at the first crab stage, and right side pleopods may be reduced or lost entirely, left side pleopods on somites 3–5 usually undergo only endopod reduction or loss. In some species of *Clibanarius* pleopod loss does not even begin until the second crab stage (Brossi-Garcia 1987, 1988). In contrast, all pleopods of *P. edwardsi* undergo dramatic reduction with the molt to the first crab stage (Fig. 1c). This type of pleopod reduction heretofore has been reported only in lithodids (i.e., Kurata 1956; Miller & Coffin 1961; Hart 1965; Crain & McLaughlin, 2000a, 2000b). Whether pleopods loss is complete in *Porcellanopagurus*, with females pleopods reappearing with maturity, as has been suggested to be the case in *Lithodes* (cf. Sandberg & McLaughlin 1998), can only be determined when a complete juvenile series becomes available for study.

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